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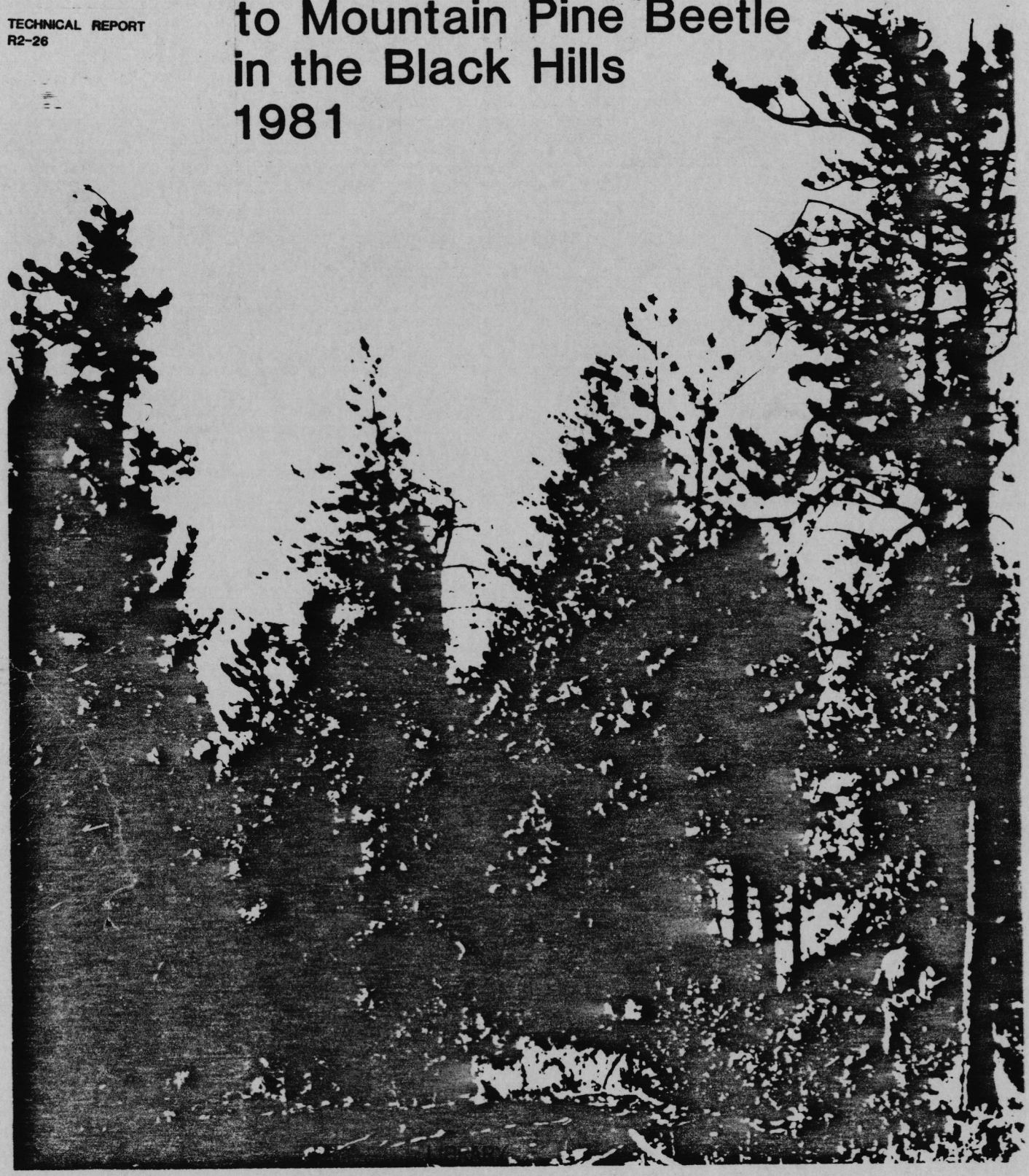
Factors Affecting Ponderosa Pine Stand Susceptibility to Mountain Pine Beetle in the Black Hills 1981



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ROCKY MOUNTAIN STATION

Mountain Pine Beetle Evaluation

Factors Affecting Ponderosa Pine Stand Susceptibility to Mountain Pine Beetle in the Black Hills

1981

by

Gene Lessard, Supervisory Entomologist

Technical Report R2-26

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Timber, Forest Pest, and Cooperative Forestry Management
Rocky Mountain Region
USDA Forest Service
11177 W. 8th Avenue
Lakewood, Colorado 80225

INTRODUCTION

The single variable most often ascribed to ponderosa pine susceptibility to mountain pine beetle attack is reduced tree vigor. The origin of this concensus is important to an understanding of current management techniques designed to increase tree vigor and reduce tree susceptibility.

Early research results suggest tree vigor is important only when beetle populations are endemic. Blackman (1931) noted that during an epidemic the mountain pine beetle does not discriminate as to the apparent health and vigor of trees attacked. In fact, the mountain pine beetle seems to show a slight preference for trees of more than average vigor. However, when endemic it breeds in trees weakened by mistletoe, lightning, or other causes. Blackman's (1931) statement regarding mountain pine beetle behavior during epidemics is confirmed by Beal (1939), who states that "During outbreaks this insect attacks vigorous, healthy trees, and frequently, as a result of its destructive work, extensive stands of pine timber are practically wiped out."

Eaton (1941) evaluated annual precipitation and excessive tree competition in relation to mountain pine beetle. He noted that "the slowing up of growth which has resulted from the interaction of these factors is indicative of a gradual weakening of the trees, which may [1/] help to explain their susceptibility to attack by the mountain pine beetle." Eaton (1941) further stated "that the mountain pine beetle tends to select, in pole stands, the weaker, less vigorous trees, particularly during periods when infestations are endemic [1/]."

Recent research does not address the concept of tree vigor during endemic and epidemic mountain pine beetle populations. In fact, the issue is clouded by Sartwell and Stevens (1975). They stated that "we agree with Eaton that intensive competition between trees at high stand densities and its effect on tree resistance to beetle attack constitute a major factor in outbreak [1/] tree killing." From their findings they chose to designate a stem basal area of 150 sq.ft. per acre as a "critical minimum"; that is the density above which stands (assuming sufficient large trees) are liable to become severely infested. They recognized that the concept of a "critical minimum" was a generalization with inherent problems.

Stevens et al. (1980) expanded on the generalization of the "critical minimum" concept. They determined that: "Stand density is arbitrarily ranked high (3), moderate (2), or low (1) when basal area of ponderosa pine stems - in trees greater than 5 inches d.b.h. - is greater than 150 square feet per acre, 80 to 150 square feet per acre, or less than 80 square feet per acre."

1/ Underlined by author

McCambridge, et al. (1982) studying epidemic mountain pine beetle noted that: "The original density of ponderosa pine correlated fairly well with trees killed by beetles, r = 0.71, but not with percent of pine killed, r = -0.001.

Original basal area of pine was less well correlated with pine trees killed, r = 0.61. The correlation with percent of trees killed was r = 0.15."

Sartwell and Stevens (1975) and McCambridge, et al. (1982) are in agreement that the more trees per acre available for infestation the more one would expect to lose if an outbreak occurs. However, McCambridge, et al. (1982) disagree with Sartwell and Stevens (1975) that reducing basal area necessarily reduces "susceptibility of stands sufficiently during outbreaks (McCambridge, et al. 1982).

Mogren (1955) studying tree resistance in epidemic mountain pine beetle populations noted "that there are ponderosa pines that are resistant to Black Hills beetle [mountain pine beetle] attack, and are able to 'pitch out' the insects even when they attack in great numbers." Resistant trees were "trees of very high vigor." He characterized resistant trees as:

1. Being taller and larger in diameter
2. Having significantly greater growth
3. Having pointed crowns
4. Having higher leader-lateral ratios
5. Having longer needles

McCambridge, et al. (1982) also noted that although all trees in some diameter classes were killed, some big trees survived. This they ascribed to random chance.

A summary of the concept of tree vigor and mountain pine beetle susceptibility is in order at this point. Note that only Blackman (1931) and Eaton (1941) contribute information on endemic populations. During endemic populations the mountain pine beetle:

1. breeds in trees weakened by mistletoe, lightning or other causes (Blackman 1931).

2. tends to select, in pole stands, the weaker, less vigorous trees... (Eaton 1941).

During epidemic populations the mountain pine beetle:

1. shows no discrimination as to the apparent health and vigor of trees attacked - at such times, indeed, seeming to show a slight preference for trees of more than average vigor (Blackman, 1931).

2. attacks vigorous, healthy trees . . . (Beal, 1939).

3. resistant trees were trees of very high vigor (Mogren, 1955).

4. tree killing (numbers of trees killed) correlated [2/] with stand density and basal area [3/] (Sartwell and Stevens, 1975; Stevens, et al. 1980; McCambridge, et al. 1982).

5. tree killing (percent of trees killed) was not correlated with stand density or basal area (McCambridge, et al. 1982)

Understanding beetle behavior under epidemic conditions does not provide information on how or why populations maintain themselves under endemic conditions. Essential to an understanding of endemic mountain pine beetle population dynamics is an understanding of the insect-host interaction.

In theory, initial infestation in a stand proceeds as follows:

Primary attack -- The host tree produces a chemical messenger which attracts mostly female mountain pine beetles (Billings, et al. 1976).

Secondary attack -- These females from the primary attack produce a complex of chemical messengers of both insect and host origin which attract large numbers of male and female mountain pine beetles (McCambridge, 1967; Pitman and Vité, 1969; Vité and Gara, 1962).

These first two processes describe the initial host selection and aggregation behavior of the mountain pine beetle. At this point the process can stop (e.g., the females produce an anti-aggregating chemical messenger) and the beetle population would be considered endemic. Or, the process could continue to:

Mass attack -- Large numbers of beetles "overwhelm adjacent trees by rapid attacks (McCambridge, 1967)." Adjacent trees may or may not be producing a chemical messenger. (The first indication of an increasing mountain pine beetle population.)

The link between host tree production of chemical messengers and tree stress has been implied but not substantiated (Waring & Pitman 1980). However, a number of different host tree conditions have been associated with primary attack. Typical associated conditions are:

2/ Since Sartwell and Stevens (1975) did not provide a correlation coefficient (r) it must be assumed that correlated in their terms means a nonstatistically tested relationship.

3/ Sartwell and Stevens (1975) and Stevens, et al. (1980) refer to stand density and basal area as interchangeable parameters.

1. root rot
2. dwarf mistletoe
3. small tree crown
4. lightning strike
5. fire damage
6. other

In the Black Hills infection by *Armillariella mellea* was found associated with nearly 90 percent of all mountain pine beetle infested trees at endemic beetle levels.[4/]

The purpose of this report is to clarify the tree selection process of the mountain pine beetle and to provide a means of estimating tree losses caused by the mountain pine beetle over time.

METHODS

The study area covered about 450,000 acres of ponderosa pine type in the northern Black Hills of South Dakota. About 1% of the study area was photographed in August 1981. Photography was 9 inch x 9 inch true color transparencies at a scale of 1:6,000. Stands were delineated on the photography and stratified by:

1. Major geologic formation

    a. Limestone Plateau
    b. Crystalline Basin
    c. Volcanic Mountains

2. Stand structure

    a. Single story
    b. Multi-story

3. Crown closure

    a. 0-25%
    b. 25-50%
    c. 50-75%
    d. 75-100%

4/ Cooperative Study - T. E. Hinds and L. R. Fuller. Black Hills Root Rot-Bark Beetle Association.

4. Mountain pine beetle infestation intensity

a. endemic $\leq$ 1.0 infested trees per 10 acres
b. light 1.1-5.0 infested trees per 10 acres
c. moderate 5.1-25.0 infested trees per 10 acres
d. heavy > 25 infested trees per 10 acres

All combinations of stratification (96) were not represented on the photo sample. To represent a broad range of stand and insect conditions, 69 stands were selected for ground evaluation.

In each sampled stand, 2.5 acre sample plots were delineated on the photography and evaluated on the ground. On each plot the following data were recorded:

1. Total number, diameter (d.b.h. to the nearest 0.1 inch) and crown ratio of infested trees by infestation class:

a. 1981 infested
b. 1980 infested
c. 1979 infested

2. Uninfested tree diameter and basal area (all tree species) from five variable plots (10 BAF); one center plot and four plots at cardinal directions.

3. Slope (%) and aspect (degrees)

4. Age and height of three dominant or codominant ponderosa pines

Significant differences in infestation level were found between the limestone plateau and the volcanic mountains and, the limestone plateau and the crystalline basin but not between the Volcanic Mountains and the Crystalline Basin (Lessard 1981). These differences were directly related (r^2 = .92) to stand structure and indirectly related to geologic formation. The limestone plateau consisted primarily of even-aged stands (69%) with an average of 18.3 infested trees per acre (Table 1). The volcanic mountains and crystalline basin contained fewer even-aged stands with a corresponding decrease in infested trees per acre (Table 1). Because of the relationship between stand structure and infestation intensity, plots from all geologic strata were combined.

Table 1. Percent of stands surveyed by stand structure and geologic formation.

Stand Structure	Geologic Formation			
	Limestone Plateau	Volcanic Mountains	Crystalline Basin	Total
	----------Percent----------			
Balanced Uneven-aged	17.2	10.0	25.0	17.4
Even-aged	69.0	45.0	25.0	49.3
Irregular Uneven-aged	13.8	45.0	50.0	33.3
Mean Trees 1/ Per Acre Infested	18.3	7.3	4.6	

1/ From Lessard 1981

Diameter distributions (proportion of trees by two inch diameter classes) were matched and similar stands combined to produce a continuum of six stand structures. Stand structures A and B consisted of balanced uneven-aged stands; C and D even-aged stands; and, E and F irregular uneven-aged stands. The effect of the mountain pine beetle in relation to stand structure was evaluated at the endemic, increasing, decreasing and epidemic phases of the mountain pine beetle:

1. Endemic -- less than one infested tree per acre per year

2. Increasing (Decreasing) -- greater than one infested tree per acre per year; less than ten percent of a stand infested over a three year period.

3. Epidemic -- greater than ten percent of a stand infested over a three year period.

Two assumptions made during data analysis were (1) that an infestation curve over time is bell-shaped. This implies that the rate of increase in infestation equals the rate of decrease. (2) the average time for an infestation in a stand is 9 years. Since mountain pine beetle infestations are modified by external factors (weather, predation, parasitism, etc.), these assumptions will seldom hold up in nature. However, they provide a base model for infestation trend prediction.

RESULTS AND DISCUSSION

Blackman (1931) and Beal (1939) were well aware of mountain pine beetle behavior during an epidemic. They both found that during an epidemic mountain pine beetle attacks vigorous, healthy trees. This concept was expanded in the current study. Those stands and corresponding stand structures, in which the the mountain pine beetle was considered to be epidemic, were examined independently from endemic, increasing or decreasing mountain pine beetle populations.

Figure 1 (B-F)[5/] shows the relationship of stand diameter prior to epidemic infestation and mountain pine beetle caused mortality (1979-81) for epidemic mountain pine beetle populations.

During the epidemic phase, the mountain pine beetle becomes selective for trees in the diameter range of 7.1-13.0 inches. That is, the proportion of infested trees in the 7.1-13.0 inch diameter range exceeds the proportion of green trees in a stand available for infestation. This parallels the work of McCambridge, et al. (1982). They found that ca. 71% of all infested trees in the moderate to heavy infestation class were in the diameter range of about 9-15 inches; only about 58% of the uninfested trees occurred in the 9-15 inch diameter range.[6/] This preference is evident for all stands which have about 75 percent of the diameter distribution in other than the 7.1-13.0 inch diameter range.

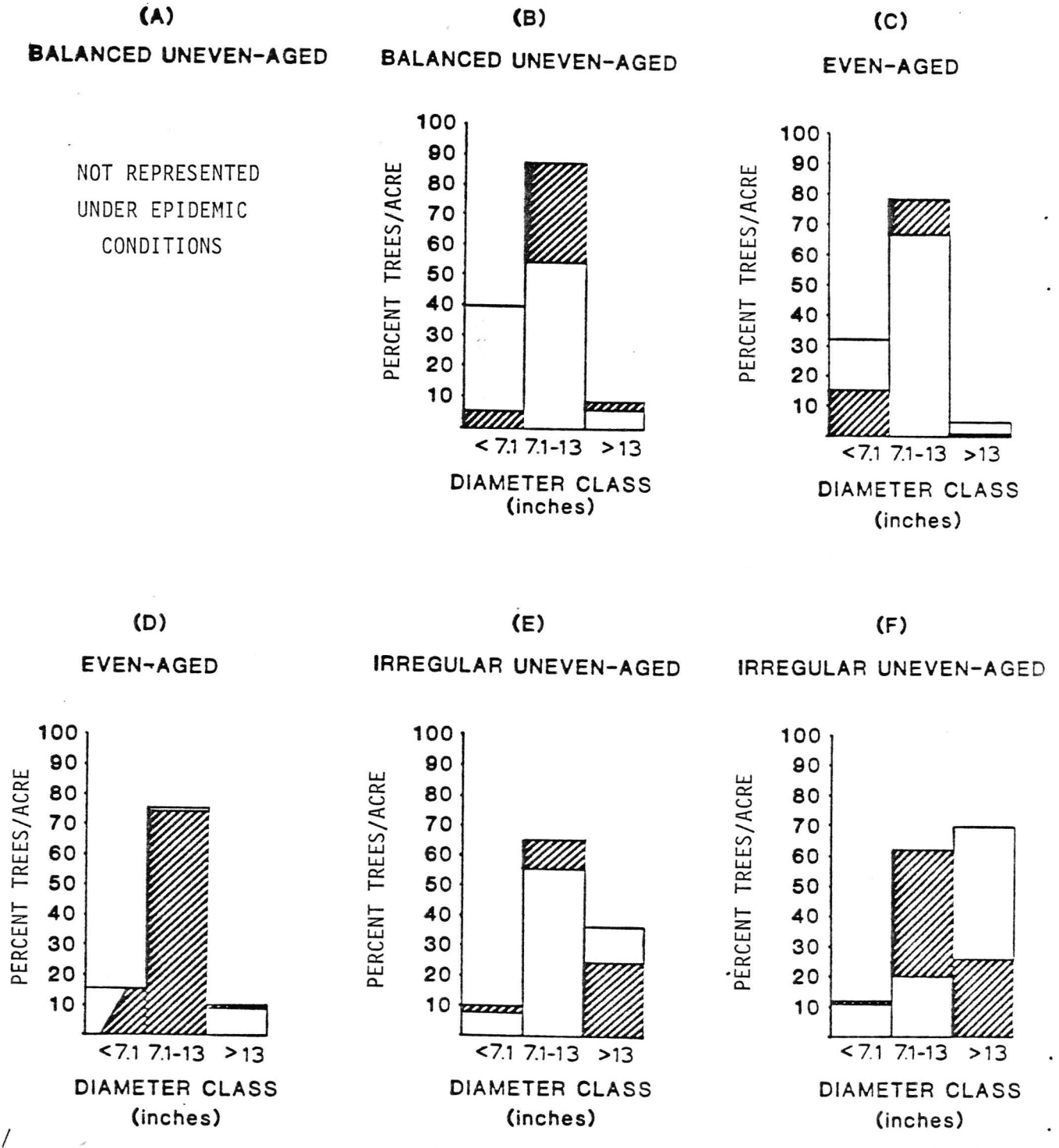
Even-aged stands sustained the highest level of infestation (Table 2). As the green stand diameter distribution shifts towards smaller average diameter (stands A-B) and larger average diameter (stands E&F), very little change in the infested stand distributions occurs. These same shifts in green stand distribution, however, show a corresponding downward shift in the level of infestation.

Although growth rates were not measured the 7.1-13.0 inch diameter range should contain the most vigorous trees in the stands examined. Alexander and Edminster (1981) found that "...the rate of diameter growth for a given GSL is not constant over time, and is essentially a negative exponential function of basal area per acre..." At the extremes they found that: "At age 63 years [an overstocked stand] contained 6,600 trees per acre with an average stand diameter of only 2.4 inches d.b.h." And, "with a 20-year cutting cycle trees reached 10.2 to 18.3 inches d.b.h. after 80 years, and 12.6 to 26.9 inches d.b.h. after 120 years for the range of GSL's [40-160] and site indexes tested." For GSL's 40 to 160 growth rate (inches per year) did not appreciably change (.13 - .23 and .11 - .22) between 80 and 120 years, respectively, though diameter increased substantially. Therefore, at about 85 sq.ft. basal area, trees in the diameter range of 7.1 - 13.0 inches would be expected to have growth rates at or above the average maximum expected growth.

5/ Stand structure A was not represented at epidemic levels.

6/ Personal communication (McCambridge).

Figure 1 -- Diameter distribution of trees/acre in the original stand [1] ☐ prior to epidemic [2] infestation and diameter distribution of infested trees per acre [3] ▨ during epidemic infestation (3 year period).



1/ Percent trees per acre in the original stand based on total trees per acre in the original stand.

2/ Percent infested trees per acre based on total infested trees per acre in the stand.

3/ Equal percentages in <7.1 inch diameter class in even-aged stand structure (D)

Table 2. Trees per acre infested (3 yr. period) by stand structure during epidemic phase. (Stands A-F Table 2 correspond to Stands A-F Figure 1).

Stand Structure	Trees per acre Infested
A - balanced uneven-aged	0.0
B - balanced uneven-aged	30.9
C - even-aged	51.9
D - even-aged	54.9
E - irregular uneven-aged	27.8
F - irregular uneven-aged	9.7

Since the greater portion of infested trees occur in the 7.1 - 13.0 inch diameter range regardless of stand structure, the relationship can be used to estimate tree losses to the mountain pine beetle.

To estimate the expected percent infestation (t) in a given stand for the epidemic phase use the following formula:

$$t = 21.15 - 61.53X + 113.76Y - 59.06Z \; ; \; r2 = 0.72$$

where t = expected percent infestation (3 years)

$X = P_{7.1\text{-}9.0}$ proportion of green trees in the 7.1 - 9.0 inch diameter class to a 3.1 inch minimum

$Y = P_{9.1\text{-}11.0}$ proportion of green trees in the 9.1 - 11.0 inch diameter class

$Z = P_{11.1\text{-}13.0}$ proportion of green trees in the 11.1 - 13.0 inch diameter class.

There is a strong association between trees infected with Armillaria root rot and endemic levels of mountain pine beetle in the Black Hills. Since Armillaria has no apparent preference for tree diameter, no such preference for tree diameter by the mountain pine beetle at the endemic level would be expected. Infested trees occurred in all stand structures (Table 3). Though some stand structures showed a preference by the mountain pine beetle for the 7.1-13.0 inch diameter class, this preference could not be demonstrated statistically. During "Primary Attack" the mountain pine beetle appears to be selective for host trees which have been weakened by stress; in this case Armillaria root rot.

The switch from endemic to an increasing population occurs when mass attack occurs. Initially, the attack is random with respect to tree diameter. However, attack is directed in that trees nearest the original host tree become infested. The original host tree then becomes the center of an infestation group. If the groups are small 6.9 ± 2.9 ($\bar{x} \pm t.05$ SE) trees per group over three years, the infested tree diameters tend to mimic diameter distribution of the original stand (Figure 2A-D). However, some preference for the 7.1 13.0 inch diameter range is evident in the irregular

uneven-age stands in Figure 2 (E-F). The greatest loss in trees per acre occurred in even-aged stand structure (C) (Table 4).

Table 3. Trees per acre infested (3 yr. period) by stand structure during endemic phase.

Stand Structure	Trees per Acre Infested
A - balanced uneven-aged	2.3
B - balanced uneven-aged	2.4
C - even-aged	1.5
D - even-aged	2.0
E - irregular uneven-aged	0.8
F - irregular uneven-aged	0.8

Table 4. Trees per acre infested (3 yr. period) by stand structure during increasing (decreasing) phase. (Stands A-F Table 4 correspond to Stands A-F Figure 2).

Stand Structure	Tree per Acre Infested
A - balanced uneven-aged	7.6
B - balanced uneven-aged	6.4
C - even-aged	14.9
D - even-aged	6.9
E - irregular uneven-aged	7.0
F - irregular uneven-aged	3.5

To estimate the expected percent infestation (t) in a given stand for the increasing or decreasing phase use the following formula:

$t = -0.19 + 7.22X + 3.39Y + 10.36Z$; $r^2 = 0.72$

where t = expected percent infestation (3 yrs)

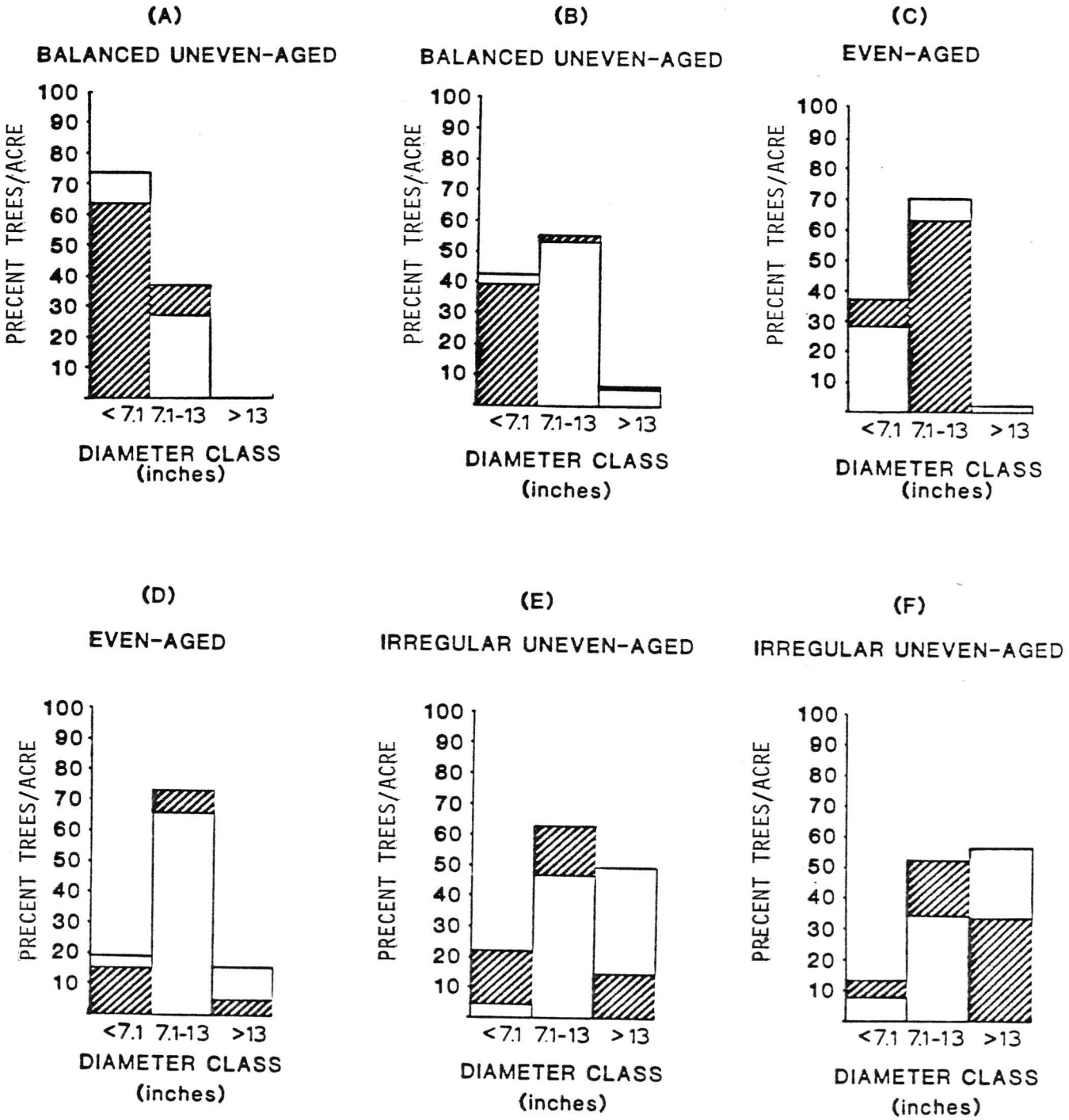
$X = P_{7.1\text{-}11.0}$; proportion of green trees in the 7.1-11.0 inch diameter class to a 3.1 inch minimum.

$Y = P_{11.1\text{-}15.0}$; proportion of green trees in the 11.1-15.0 inch diameter class

$Z = P_{15.1\text{-}19.0}$; proportion of green trees in the 15.1-19.0 inch diameter class

The results of this study confirm the observations of McCambridge, et al. (1982) for epidemic mountain pine beetle populations (Table 5). There is a relationship between infested trees per acre, original stand density and, original stand basal area. However, the relationship is not strong.

Figure 2 -- Diameter distribution of trees per acre in the original stand [1] □ prior to increasing or decreasing infestation and diameter distribution of infested trees per acre [2] ▨ during increasing or decreasing infestation (3 year period).



[1] Percent trees per acre in the original stand based on total trees per acre in the original stand.

[2] Percent infested trees per acre based on total infested trees per acre in the stand.

Table 5. Coefficient of correlation (r) between stand density and basal area with mountain pine beetle infestation level

Dependent Variable	Independent Variable	Correlation Coefficient Infestation Level			
		Endemic	Increasing (Decreasing)	Epidemic	McCambridge, et al. 1982
Stand Density (Trees/Acre)	Infested Trees/Acre	0.36	0.16	0.72	.71
Stand Density (Trees/Acre)	Percent Infested Trees/Acre	0.41	0.59	0.21	.001
Stand Basal Area/Acre	Infested Trees/Acre	0.30	0.26	0.65	.61
Stand Basal Area/Acres	Percent Infested Trees/Acre	0.35	0.31	0.15	.15

Stand density and basal area are not the cause of mountain pine beetle outbreaks. Data in Table 6 support this thesis. No significant differences ($P < .05$) were found among infestation levels and stand density expressed as trees per acre or basal area. Significant differences ($P < .05$) were found among all infestation levels and trees per acre infested and among infestation levels and percent trees per acre infested.

Table 6. Comparison of stand density and basal area with mountain pine beetle infestation level

Infestation Level	No. of Stands	Stand Density		Infested Trees	
		Trees/Acre (#)	Basal Area (sq.ft.)	Trees/Acre (#)	Percent Trees/Acre (%)
		Mean $\pm$ $t_{.05}SE$			
Endemic	31	160.0 $\pm$ 55.1	85.4 $\pm$ 10.6	1.5 $\pm$ 0.3	1.3 $\pm$ 0.2
Increasing (Decreasing)	24	183.9 $\pm$ 58.9	84.8 $\pm$ 13.7	6.9 $\pm$ 1.3	5.1 $\pm$ 0.9
Epidemic	14	148.5 $\pm$ 48.6	84.4 $\pm$ 21.6	41.0 $\pm$ 24.7	25.5 $\pm$ 7.3

The relationship between stand density, basal area, and mountain pine beetle can be simply stated: The more trees available for infestation, in the 7.1 - 13.0 inch diameter class, the more trees one would expect to lose given the occurrence of an infestation.

CONCLUSIONS

The most susceptible stands to the mountain pine beetle in the Black Hills are even-aged stands with ca. 75 percent or more trees in the 7.1-13.0 inch diameter range. Susceptibility decreases as the distribution of trees shifts to smaller and larger diameter ranges.

In the endemic phase of infestation, mountain pine beetle attack is directed primarily towards trees infected by Armillaria root rot and secondarily by trees weakened by other agents. As mountain pine beetle attack increases from the endemic phase or decreases to the endemic phase, attack becomes random. All diameter classes from 7.1-19.0 inches are equally susceptible. During the epidemic phase, mountain pine beetle attack becomes directed towards trees in the diameter range of 7.1-13.0 inches. The mountain pine beetle tends to convert even-aged stands to irregular uneven-aged stands and maintains stands in the uneven-aged configuration due to this mid-range diameter tree mortality.

SILVICULTURAL IMPLICATIONS

Since Armillaria root rot is prevalent, particularly in managed stands, in the northern Black Hills, endemic and low level mountain pine beetle populations are expected in all managed stands regardless of stand configuration. However, the impact of epidemic mountain pine beetle damage can be prevented or substantially reduced through silvicultural techniques. These techniques involve variations in even-aged and uneven-aged management.

Creating extensive areas occupied by even-aged stands in the susceptible diameter range leads to large scale epidemics of mountain pine beetle. If even-aged management is to be the preferred management alternative then management areas should be broken up into a matrix of 30-50 acre stands with a wide spectrum of age classes. Small highly susceptible stands are easier to monitor and require less reaction time and control effort should an epidemic develop. Also, the area diversity created will enhance all resource values.

Uneven-aged stand management may be preferable in areas where access is limited or re-entry is not scheduled in the near future (ca. 40 years). Uneven-aged stands are less likely to sustain a mountain pine beetle epidemic than even-aged stands. If an epidemic does occur in an uneven-aged stand, losses to the mountain pine beetle will be in the order to 30-50% less than the most susceptible even-aged stand with comparable stocking.

RESEARCH AND EVALUATION NEEDS

A number of research and evaluation needs surfaced during this evaluation. These are listed with a brief description.

1. Determine the relationship between insect and host during primary attack.

   - There is a need to understand the changes in host tree chemistry associated with tree stress and the response of the mountain pine beetle to these chemical changes. This could lead to strategies for manipulating the host tree or beetle at endemic levels.

2. Develop a stand risk rating system for ponderosa pine regionwide.

   - The results of this evaluation need to be validated on a regionwide basis. Validation will require a series of fixed plots which can be monitored over a period of at least 10 years.

3. Develop an economic model based on the regression equations developed in this evaluation.

   - Using the loss estimators in this evaluation, develop a yield model which will incorporate expected loss over rotation and the consequent economic impact. Update the loss estimators based on information from (2) above.

4. Integrate the stand risk rating system into the Stage II data collection and analysis system.

   - Provide stand risk as an integral part of Stage II printouts. This will assist land managers prioritize timber sale programs.

5. Develop and test silvicultural systems to reduce stand susceptibility to mountain pine beetle.

   - Silvicultural systems need to be developed which will reduce stand susceptibility to mountain pine beetle while enhancing featured resource values.

6. Develop management strategies to reduce the levels of Armillaria root rot in managed stands.

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